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THE FAUNA OF ATLANTIC MARINE CAVES: EVIDENCE OF DISPERSAL BY SEA FLOOR SPREADING WHILE MAINTAINING TIES TO DEEP WATERS

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Abstract.—Evidence is presented that significant ties exist between the faunas of marine caves and those of the deep seas, that marine cave faunas may contain very old elements, and that marine caves have served as faunal refuges over very long periods of time. In addition, the term "*crevicular*" is introduced to designate those aquatic habitats formed by crevasses in and among rocks, as well as to describe the organisms that live in those habitats.

We feel that data recently gathered in Bermuda, the Bahamas, the Turks and Caicos, Ascension, and the Canary Islands (Fig. 1) shed light on some of the puzzling distributional patterns noted for cavernicolous crustaceans found on oceanic islands of the Atlantic and the Pacific, and bear generally on sea floor spreading.

In our work we have been dealing exclusively with (and drawn our conclusions from) invertebrates—primarily shrimps—that inhabit anchialine waters and marine caves. That is, waters having no surface connection with the sea, but which nevertheless contain salt or brackish water the level of which fluctuates with the tides.

Sket and Iliffe (1980) summarized information then available on the fauna of the caves of Bermuda, and reported that pools in the caves were inhabited by a wide variety of marine invertebrates—ranging from ciliates to tunicates. In discussing the zoogeographical affinities of the cave fauna of the island, they noted striking zoogeographical connections between Bermuda and the east, and commented on four theories that had been proposed to explain the distribution of marine cave organisms:

1) Plate tectonics, as stated by Sterrer (1973) for interstitial fauna, was discussed and partially rejected because Bermuda had never been a part of the continental plates.
2) Stranding on the shoreline of receding fossil seas, as suggested by Stock (1977), was ruled out because Bermuda was too young to have experienced significant shoreline changes.
3) Connections with the abyssal depths, as suggested by Webb (in Sterrer 1973), was discounted because it was felt that changes in meiofauna with depth and substrate indicated that such interconnections were unlikely. Also, at that time no abyssal species had been identified from the caves.
4) Drifting on flotsam was deemed to be a possibility for short distances—such as from the Caribbean—but Bermuda was close enough to Africa for this to have been feasible only for a comparatively short time after the island was formed, about 110 million years ago.

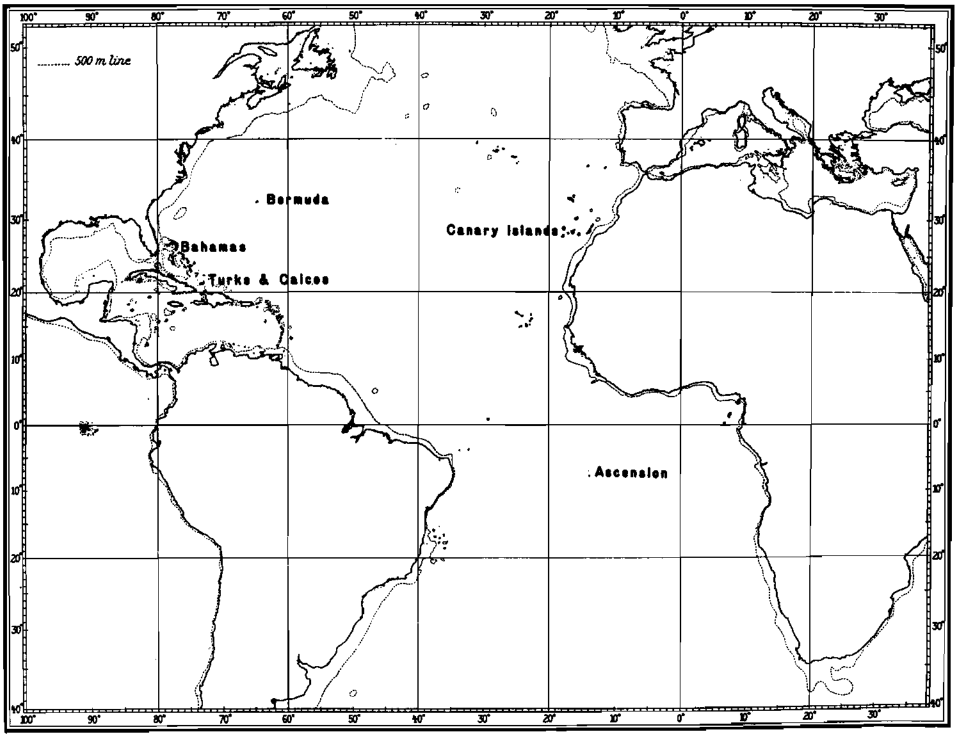

Fig. 1. Map showing Atlantic and Caribbean islands or island groups from which the organisms discussed in this paper were taken.

Since the Sket and Iliffe paper appeared, only four years ago, additional data have been gathered on the caves of Bermuda, the Turks and Caicos, the Bahamas, and the Canary Islands that allow us to expand on these observations—particularly as they relate to shrimp distributions and to abyssal connections.

With some of the cave organisms, it might be easy to believe that they could reach Bermuda through oceanic dispersal of pelagic larvae. The occurrence of species on Bermuda that are widespread in similar habitats in the Caribbean is such an example. However, the fact that we do not yet know if those shrimp produce pelagic larvae weakens such an hypothesis.

With other cave shrimps, however, it is even more difficult to create a scenario for their dispersal. *Typhlatya iliffei* Hart and Manning, 1981, endemic to Bermuda, has as its closest relative *Typhlatya rogersi* Chace and Manning, 1972—a species that is endemic on Ascension Island in the Southern Atlantic. The remaining representatives of the genus occur in subterranean fresh waters of Caribbean islands, Mexico, Central America, and the Galapagos.

The genus *Procaris* was described from Ascension Island by Chace and Manning (1972) and the following year Holthuis (1973) described another species belonging to the genus from Hawaii. Only recently a third species has been found on Bermuda (Hart, Manning, and Iliffe, in prep.).

The distributions of these species, as well as that of the *Ligur-Barbouria-Somersiella* complex spanning the Atlantic from the Mediterranean to Bermuda and the Caribbean (Manning and Hart 1984), lead us to give added credence to the deep-sea ties of these species, as well as emphasizing the hypothesis that some of the island species may represent relicts of ancient stocks.

Our investigations have revealed a number of examples leading to these conclusions, and a survey of the literature has yielded others. With regard to deep-sea ties, the following seem relevant:

1) Material recently collected in a Bermuda cave by Iliffe contained a representative of a new order of Peracarida (Bowman and Iliffe 1985). Almost simultaneously, a closely related species was collected in the open ocean at a depth of 1000 meters. (Sanders, Hessler, and Garner 1985).
2) A new halocyprid ostracod that has been found in a Bermuda cave is considered by Martin Angel (personal letter to Iliffe) to be intermediate between the undoubtedly ancient Thaumatocyprididae and the Halocyprididae. Angel suggests that this indicates the cave faunas to be important links in establishing the evolution of the present oceanic faunas.
3) An undescribed polychaete from a cave in the Turks and Caicos, representative of a group otherwise known from deep waters, is presently being described by Marian Pettibone.
4) A new ostracod from the Turks and Caicos, with deep sea relatives, is being described by L. S. Kornicker.
5) A new shrimp family from the Turks and Caicos, related to the bresiliid shrimp recently described from the thermal vents of the Galapagos Rift (Williams and Chace 1982), is being described by Hart, Manning, and Iliffe (in prep.).
6) A species of *Munidopsis* (*M. polymorpha* Koelbel), a speciose genus otherwise known from shelf, slope, and abyssal depths (Doflein and Balss 1913), is among the inhabitants of a lava tube formed 3000–5000 years ago in Lanzarote, Canary Islands. Wilkens and Parzefall (1974) suspect that this shrimp and other inhabitants of the lava tube might be widespread in the neighboring Atlantic. Miyake and Baba (1970), in their list of the known West African species, gave no records for this species outside of caves.
7) Another inhabitant of that lava tube is a species of the amphipod genus *Spelaeonicippe,* family Pardaliscidae, which, as pointed out by Stock and Vermuelen (1982:4), "are predominantly bathyal/abyssal/hadal, pelagic Amphipoda." These same authors described a second species of this genus from waters of a limestone cave on Providenciales, Turks and Caicos.
8) In addition, Pettibone (1976) discussed a polynoid polychaete, *Gesiella jameensis,* from the same lava tube. The polychaete belongs to a subfamily otherwise known only from deep water.
9) And three other genera—*Barbouria, Ligur,* and *Somersiella*—known primarily from anchialine or cave habitats point in the same direction. Four of the five species assigned to these genera occur only in these habitats, but the type-species of *Ligur* is a deep-sea species, known only from shelf-slope depths.

As for the possible antiquity of some crustacean species, J. Tuzo Wilson (in litt.) suggested that "it is just conceivable that forms of life might have survived on Ascension from the time when the Atlantic was very narrow and the forerunners of Ascension were in contact with Brazil and the Cameroons."

Following on this, Hobbs and Hart (1983), in a review of the genus *Atya*, found that two species—*A. gabonensis* and *A. scabra*—are identical on both sides of the Atlantic, and that *Atya intermedia* (inhabiting two islands in the Gulf of Guinea) is so similar to *Atya innocous* (inhabiting the Greater and Lesser Antilles and Central America) that they were reluctant to recognize them as separate species. They noted that these shrimps must be considered little, if at all, changed since the Africa-America continental masses were still approximate—suggesting that this group of shrimps is extremely old, dating from at least the Middle Jurassic, 175 million years ago.

And finally, Iliffe, Hart, and Manning (1983) hypothesized that part of the cavernicolous invertebrate marine fauna of Bermuda represent groups that survived on submerged or emergent sea mounts along the Mid-Atlantic Ridge since the early Mesozoic, and that geothermal activity may have maintained water temperatures in caves sufficiently high to protect certain species during periods of glaciation.

Conclusions

We believe that the evidence presented here supports the conclusions 1) that there are significant ties between the marine cave fauna and the fauna of the deep sea, 2) that the cave faunas may contain very old elements, and 3) that caves have served as refuges over very long periods of time.

It seems likely that the subterranean habitats on ocean islands consist not only of caves, but of crevicular habitats in the rock—similar environments that are potentially available for colonization anywhere in the water column. Thus, while surface caves and pools in limestone may be relatively young, the actual habitat may be as old as the island on which it is found.

We use the term "crevicular" to designate those aquatic habitats formed by crevasses in and among rocks. We also use it to describe the organisms that live in those habitats. For the purposes of this definition, a cave sensu stricto is simply a large crevass, or it may be merely the gateway through which smaller crevasses are made accessible to the student of crevicular organisms. The crevicular habitat differs from the interstitial habitat primarily in size, and the animals that live in both habitats are likely to be thigmotactic.

Following on this, it seems probable that species, or species-groups, could form a continuum—reaching from the caves of one island into the deep waters via the natural crevasses among rocks and so on up the slopes of other islands or continental masses.

One does not have to wander far from that idea to see that if crustacean species are as conservative as some appear to be, then the actual spreading of the sea floor could be a means by which some species have achieved their present day distributions.

Indeed, Chace and Hobbs' (1969:21) tongue-in-cheek proposal of a "continuous spelean corridor" between islands may not be so far-fetched after all.

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